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Original Articles

Extended patchy ecosystems may increase their total biomass through self-replication

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ABSTRACT

Patches of vegetation consist of dense clusters of shrubs, grass, or trees, often found to be circular characteristic size, defined by the properties of the vegetation and terrain. Therefore, vegetation patches can be interpreted as localized structures. Previous findings have shown that such localized structures can self-replicate in a binary fashion, where a single vegetation patch elongates and divides into two new patches, in a process resembling cellular mitosis. Here, we extend these previous results by considering the more general case, where the plants interact non-locally, this extension adds an extra level of complexity and shrinks the gap between the model and real ecosystems, where it is known that the plant-to-plant competition through roots and above-ground facilitating interactions have non-local effects, i.e. they extend further away than the nearest neighbor distance. Through numerical simulations, we show that for a moderate level of aridity, a transition from a single patch to periodic pattern occurs. Moreover, for large values of the hydric stress, we predict an opposing route to the formation of periodic patterns, where a homogeneous cover of vegetation may decay to spot-like patterns. The evolution of the biomass of vegetation patches can be used as an indicator of the state of an ecosystem, allowing to distinguish if a system is in a self-replicating or decaying dynamics. In an attempt to relate the theoretical predictions to real ecosystems, we analyze landscapes in Zambia and Mozambique, where vegetation forms patches of tens of meters in diameter. We show that the properties of the patches together with their spatial distributions are consistent with the self-organization hypothesis. We argue that the characteristics of the observed landscapes may be a consequence of patch self-replication, however, detailed field and temporal data is fundamental to assess the real state of the ecosystems.

1. Introduction

Spontaneous shift from a uniform cover of vegetation into a fragmented ecosystem constituted by a spatially periodic distribution of gaps, or patches, is a well documented issue in plant ecology. This transition may occur either in water or nutrient limited territories. It is now widely admitted that facilitative and competitive interactions between individual plants can directly or indirectly account for the formation of vegetation patterns (Lefever and Lejeune, 1997; Klausmeier, 1999; HilleRisLambers et al., 2001; von Hardenberg et al., 2001; Tlidi et al., 2008; Vesipa et al., 2015). The spatial distribution of such patterns can be modified by the effect of climatic, terrain and anthropogenic influences (Kefi et al., 2007; Kefi et al., 2007; Dakos et al., 2011; Deblauwe et al., 2012). Quantitative studies based on field observations have been made on: the Sahelian gapped patterns, constituted by Combretum micranthum trees (Barbier et al., 2006; Barbier et al., 2008; Lefever et al., 2009); patches of vegetation in arid high altitude environments in the tropical alpine ecosystems of the Andes formed by Festuca orthophylla (Poaceae); and for grasses or by Pycnophyllum tetrastichum cushions (Bolivia, Couteron et al., 2014).

Patterned vegetation landscapes are fragmented, i.e, the terrain is only partially covered by vegetation. Some of these landscapes are composed of vegetation patches, which may be sparsely or regularly distributed. These patches usually have a characteristic size and well defined circular shape. It has been shown recently that localized patches can be destabilized by a deformation of their circular shape, either leading to the formation of labyrinthine patterns (Bordeu, 2016), or dividing into two new identical patches of smaller diameter (Bordeu

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et al., 2016). The latter is a phenomenon often called self-replication and resembles mitotic cell division. It has been studied in the context of herbaceous populations in arid ecosystems (Bordeu et al., 2016). The self-replication mechanism allows the transition from a single localized structure into a qualitatively different state, namely a hexagonal periodic pattern of vegetation. During the transition from localized to periodic pattern, the total biomass increases as newly formed patches contribute to the repopulation of the territory accessible to vegetation. From a theoretical point of view, self-replication is a patterning phenomenon better known in physico-chemical contexts rather than ecological systems. It is a generic mechanism of pattern formation, which has been observed and established in various non-equilibrium systems, such as chemical systems (Pearson, 1993; Lee et al., 1994; Kaminaga et al., 2005; Kolokolnikov and Tlidi, 2007), in plant ecology (Meron et al., 2004; Bordeu et al., 2016, and nonlinear optics Tlidi et al., 2002).

In this contribution, we investigate the space-time dynamics of vegetation under a self-replication phenomenon by extending the previous work by Bordeu et al. (2016), Bordeu (2016), where a simple local model was used to illustrate that self-replication was a possible mechanism for vegetation propagation. Here we consider a general integro-differential model instead of the simplified model of Bordeu et al. (2016), Bordeu (2016), where non-local interactions are taken explicitly into account. The non-localities arise from the facilitating mechanisms, i.e. promoters of vegetation growth, competition mechanisms, which limit vegetation growth, and dispersion effects. This model corresponds to a variant of the theory of vegetation patterning established by Lefever and Lejeune (1997), which focuses on the relationship between the structure of individual plants and the facilitation-competition interactions existing within plant communities. It is now widely recognized that the existence of facilitation and competition interactions play an important role in the formation of self-organized vegetation patterns. Numerical simulations of our model show indeed a self-replication process that leads moderately arid ecosystems to undergo a transition to higher biomass states, namely hexagonal patterns of vegetation patches. Moreover, we show that this kind of patterns may be obtained through the decay of a homogeneous vegetated landscape towards a less populated fragmented state, where hydric stress induces contraction of vegetated areas. Depending on the levels of aridity, the ecosystems may decay to a different type of patterned states or even become desert.

We study the characteristics of both self-replication and fragmentation processes through the analytic and numerical analysis of a general integro-differential model. We show, from a theoretical perspective, that depending on the levels of aridity localized patches can be more or less stable than the periodic pattern, a phenomenon previously studied in simpler local models (Vladimirov et al., 2011). In an attempt to conciliate the theoretical observations with real data, we consider two ecosystems, namely, from Zambia and Mozambique, these landscapes are composed of vegetation patches reaching large sizes, of the order of tens of meters in diameter (see Fig. 1). We perform statistical analysis of satellite images and find that patches have correlated characteristic patch sizes and inter-patch distances along with other properties that support the hypothesis of the self-organization nature of these landscapes.

The article is organized as follows: in Section 2.1 the theoretical model is introduced, together with the phase diagram. A description of the methods used to analyze the satellite images are included in Section 2.3. The results are presented in Section 3. Theoretical results indicating the relationship with the wavelength and the range of the facilitative and competitive interactions are presented in the appendix. Finally, we present the Discussion, Conclusions and Perspectives of our work.

2. Methods

2.1. Mathematical model

The modeling of ecosystems is a challenging and complex problem. Here, we adopt the theory of vegetation patterns established by R. Lefever and coworkers two-decades ago to model the spatiotemporal dynamics of vegetation in which both space and in time are considered to be continuous variables (Lefever and Lejeune, 1997). This theory incorporates the non-local facilitative and the competitive plant-to-plant interactions though kernels (Lefever and Lejeune, 1997; Tlidi et al., 2008; Lefever et al., 2009; Lefever and Turner, 2012). In the absence of these interactions, the resulting model is similar to the paradigmatic logistic equation introduced by Verhulst to study population dynamics (Verhulst, 2013; Mawhin, 2002). In what follows we consider vegetation of a single species settled on a flat landscape under isotropic and homogeneous environmental conditions. To simplify further the description of the system, we assume that all plants are mature. Thus, we neglect age classes. This approximation can be justified by the fact that individual plants grow on much faster time scale comparing to the time scale of the formation of regular vegetation pattern. The only variable is the vegetation biomass density which is defined at the plant level. Let us introduce the biomass density, $b(\mathbf{r},t)$, that satisfies the following dynamical evolution (Tlidi et al., 2008; Lefever et al., 2009)

$$\partial_t b(\mathbf{r},t) = b(\mathbf{r},t)[1-b(\mathbf{r},t)]M_f(\mathbf{r},t)-\mu b(\mathbf{r},t)M_c(\mathbf{r},t) + DM_d(\mathbf{r},t), \tag{1}$$

where $\mathbf{r}$ and t are the spatial coordinates and time, respectively. The time derivative is represented by ∂_t. The parameter μ, is the decay-to-growth rate ratio. It can be viewed as an indirect measure of resource scarcity or stress, that limits net biomass production and is what we refer to as aridity parameter. The first and the second terms on the right-hand-side of Eq. (1) account for the plant-to-plant facilitation and competition feedbacks, respectively. They describe the spatial extension of feedback effects in terms of the characteristic ranges L_f and L_c over which facilitative and competitive interactions operate, respectively. The facilitative interaction acts on the level of the aerial plant structure (crown) that involves sheltering, litter, water funneling or any other effect, such as seed production and germination that contribute to the

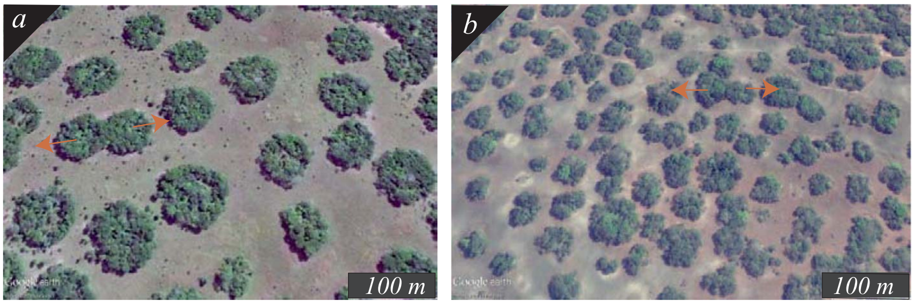

Fig. 1. Satellite images (*Google Earth Pro*), of vegetation patches in (a) the Mufumbwe District in the North-Western Province of Zambia [13°46′39.83″S, 25°16′39.59″E], and (b) the Fombeni, Mozambique [18°41′02.17″S, 35°31′55.95″E]. The red arrows indicate overlapping patches, possibly undergoing self-replications.